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*Published in:*  
Ibis

*DOI:*  
[10.1111/j.1474-919X.2011.01170.x](https://doi.org/10.1111/j.1474-919X.2011.01170.x)

**IMPORTANT NOTE:** You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2011

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Piersma, T. (2011). From Spoonbill to Spoon-billed Sandpiper: The perceptual dimensions to the niche. *Ibis*, 153(4), 659-661. <https://doi.org/10.1111/j.1474-919X.2011.01170.x>

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## Commentary

# From spoonbill to Spoon-billed Sandpiper: the perceptual dimensions to the niche

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According to Begon *et al.* (2006), a niche is not a place but an idea. A niche is a summary of an animal's tolerances and requirements. This determines where an animal would do best and where it likes to be; in other words, how an animal would select its habitat. Habitat selection is usually represented graphically in terms of prey selection, food intake rates and predator avoidance (Piersma 2011), but when this is done for particular animal species, their morphological, physiological, behavioural and sensory design features are mostly taken for granted (e.g. Wiens 1989, Morrison *et al.* 1990, Goss-Custard *et al.* 2006).

How helpful even a limited understanding of, in this case, prey detection mechanisms could be for predictive models of habitat selection and foraging distributions became clear early on in our work on Red Knots *Calidris canutus*. The precise arrangement of pressure sensors in the bill tip and their wiring to and in the brain explained the considerable capacity of Red Knots to detect hard objects such as bivalves and snails in wet soft sediments (Piersma *et al.* 1998). However, these sensory insights then also helped us to understand the rather low giving-up densities of available prey at some sites (Piersma *et al.* 1993), the near-absence of soft-bodied prey such as polychaete worms in their diets (Piersma 1991), and the foraging distributions of Red Knots over intertidal mudflats at a variety of spatial and temporal scales (Piersma *et al.* 1995, van Gils *et al.* 2006b, Quaintenne *et al.* 2011). Thus, if a little understanding of even a single 'design' feature helped so much to make sense of this species' ecology, imagine what an understanding of multiple design features would do (van Gils *et al.* 2006a).

This takes me back to a symposium that I once attended at Leiden University. I was there to tell the story of the specialized bill-tip organ of Red Knots and how this helped us understand their food and habitat choices. The audience consisted of functional morphologists in the tradition of Leiden's van der Klaauw (1948) and see, for example, Gerritsen & Sevenster 1985, Zweers *et al.* 1995, van der Leeuw *et al.* 2003). Apart from the widespread whisperings during the conference dinner about functional morphology rapidly becoming a dying trade, the composition of the nationalities around the table struck me as odd. Whereas the behavioural, ecological and ornithological meetings that I was used to were usually dominated by scientists from English-speaking countries, none of those were there; the audience was German, Dutch, Austrian and French only. Here were the scientists who could tell one bone, one set of muscles or one sensory organ from another and know how to study their morphology and functionality, and there we were, apparently losing these remarkable, if somewhat inward-looking, specialists.

Still, as witnessed by a steady trickle of new bird-related publications (e.g. Guillemain *et al.* 2002, Cunningham *et al.* 2010a, 2010b, Demery *et al.* 2011), the trade that merges insights from morphology, sensory physiology and ecology is alive and well. In this issue of *Ibis*, Martin and Portugal (2011) describe the visual fields of four ecologically distinct but phylogenetically related wading birds from one family, two ibises and two spoonbills, and interpret their findings in the context of the foraging ecology of these threskiornithids. They were in for a surprise when finding that even such tactile foragers with long bills have fields of vision that enables them to look binocularly at freshly captured prey. Clearly, careful scrutiny of captured prey, during handling between the tips of their mandibles before ingestion, is important enough for these spoonbills and ibises to give up the possibility of complete celestial coverage by having highly placed eyes. The ingestion of Three-spined Sticklebacks *Gasterosteus aculeatus* in full self-defence must be something like eating barbed wire. It involves the disarmament of the spines by careful head-up positioning of the fish before swallowing, and I can see why spoonbills need to use binocular visual input to do this efficiently. That spoonbills and ibises are large bodied, and thus have less to fear from avian predators than have smaller tactile-feeders such as ducks, may explain why the large wading birds have given up complete celestial vision, whereas the ducks have not (Martin 1986b, 2007, Guillemain *et al.* 2002, Martin *et al.* 2007a).

Such trade-offs are paramount in the designs of all animals, and it is tribute to Graham Martin that he has built up such an extraordinary portfolio of comparative studies at the interface between morphology, sensory physiology and ecology (e.g. Martin 1994, 2009, 2011, Martin & Katzir 1995, Martin & Coetsee 2004, Martin

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*et al.* 2007b, 2008). Starting off with studies explaining aspects of the ecology of owls with reference to their capacity to see in the dark (Martin 1984, 1986a, 1990), he went on to examine a wide variety of birds using his self-constructed avian ophthalmoscope (Martin 2007). Time and again Martin and his associates have found that, beyond the grand design features of clades of birds, the details of the perceptual systems reflect the finer details of birds' ecologies rather than shared ancestry. More often than not, studies of fields of vision hint at key ecological features that ecologists had failed to notice. For example, Eurasian Golden Plovers *Pluvialis apricaria* are known as night foragers (Gillings *et al.* 2005, Gillings & Sutherland 2007), and indeed they have very large eyes (and probably sharp ears as well, Lange 1968) to help them locate earthworms (Lumbricidae) close to and on the surface of arable fields and meadows. In fact, the eyes are so big that this has necessitated special supraorbital bones to better anchor the eyes in the eye-sockets (Martin & Piersma 2009). However, the presence of this extra bone, the eye-brow of plovers, then leads to a wide blind area above the head: the plovers cannot detect dangers coming from above and behind. This realization suddenly explained why European Golden Plovers are often so immensely cryptic in their behaviour. They are true masters of disappearance even in daytime and even in open landscapes. They do this by sitting tight on the ground (this would make them hard to locate and unavailable for Peregrines *Falco peregrinus* which do not capture prey on the ground), or by circling in flocks high in the air on warm days with thermals (again taking them out of the reach of raptors).

A remarkable avian radiation is that of the sandpipers, the Calidrinae (family Scolopacidae), ranging in size from the puny 20-g Least Sandpiper *Calidris minutilla* to the relatively mighty 200-g Great Knot *Calidris tenuirostris* (Piersma *et al.* 1996). Within this subfamily, the Great Knot (together with the much shorter-billed and rocky shore-foraging Surf-bird *Aphriza virgata*) belongs to the sister clade of Red Knots (A.J. Baker unpubl. data). When one watches Great and Red Knots foraging together in mixed flocks on mudflats in northwest Australia, doing the same sort of things and taking the same sorts of prey, one would assume that they share the same sensory tools. But closer examination shows that they do not. With respect to the bill-tip organ that makes Red Knots so special (Piersma *et al.* 1998), with far fewer and not-forwardly-directed sensory pits in the tips of the upper and lower mandible, Great Knots and Surf-birds are actually very similar, and quite distinct from Red Knots (H. Berkhoudt & T. Piersma unpubl. data). This tallies with behavioural observations on captive Great Knots, which do not appear to have the urge to spend 10–20% of the day probing soft sediments to locate prey that are never there, as is the wont of cap-

tive Red Knots (T. Piersma unpubl. data). I am quite convinced that neither Great Knots nor Surf-birds possess the remote prey detection system of Red Knots. However, they may not be as 'blind' to vibrations made by burrowing worms and shrimp as Red Knots are, a sensory modality that appears to be the specialization of Sanderling *Calidris alba* (Gerritsen & Meijboom 1986).

Then there exists the fantastic morphological spoon-bill-like bill specialization of the critically endangered Spoon-billed Sandpiper *Calidris/Eurynorhynchus pygmaeus* (Piersma 1986, Taldenkov & Gerasimov 2006), but by and large sandpiper bills are rather uniform in shape and size. I suggest that the evolutionary radiation of sandpipers to large extent is a radiation of the bill-tip organ. Comparative studies of that organ, in combination with other sensory modalities such as taste (Gerritsen *et al.* 1983) and vision, as explored by Martin and Portugal in this issue of *Ibis*, could generate considerable and unexpected insights into the ecology and distribution of this group of birds. In fact, I believe that future studies in avian biology that deal with daily activity rhythms, foraging distributions, habitat selection and indeed the niche will always profit from taking the perceptual characteristics of the focal species seriously into account.

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